264

Myrmotherula hauxwelli/ M. guttata

6 Gymnopithys leucaspis/G. rufigula Tyranneutes stolzmanni/

Cyanocorax violaceus/C. cayanus

4,15 Euphonia rufiventris/ E. cayennensis

6,15 Euphonia laniirostris E. violacea

NW Colombia-E Panama

6 Aramides wolfi/A. cajanea

2,6,12 Crax rubra/C. alberti

4 Pionopsitta pulchra/P. haematotis

6 Trogon comptus/T. melanurus 5,6 Ramphastos brevis/R. vitellinus

citreolaemus/R. sulfuratus
6 Formicarius nigricapillus/F. analis

6 Pittasoma rufopileatum/P. michleri

1,4,6 Pipra mentalis|P. erythrocephala 1,6 Rhynchocephalus brevirostris|

R. olivaceus

6 Campylorhynchus albobrunneus/ C. zonatus

6 Psarocolius cassini/P. guatimozinus

15 Tangara lavinia | T. gyrola 6,15 Cyanerpes caeruleus | C. lucidus 6,15 Heterospingus xanthopygius |

H. rubrifrons

Central America

Phloeoceastes guatemalensis|
P. melanoleucus
Dysithammus puncticeps|
D. striaticeps
Synallaxis erythrothorax|
S. brachyura

15 Lanio aurantius/L. leucothorax

15 Ramphocelus passerinii/ R. flammigerus

15 Thraupis abbas | T. palmarum 15 Euphonia affinis | E. luteicapilla

Australia

Malurus elegans|M. pulcherrimus|
M. lamberti
Sericornis cautus|S. pyrrhopygius
Sericornis beccarii|S. magnirostris
Acanthiza pusilla|A. apicalis
Acanthogenys rufogularis|A. chrysoptera
Lichenostomus fuscus|L. flavescens
Melithreptus albogularis|M. lunatus
Ramsayornis modestus|R. fasciatus
Pardalotus punctatus|P. xanthopygius
Poephila acuticauda|P. cincta
Chlamydochera maculata|C. nuchalis
Cracticus torquatus|C. mentalis

Turnix varia | T. olivii Petrophassa albipennis | P. rufipennis Calyptorhynchus funereus | C. baudinii Calyptorhynchus magnificus | C. lathami Cacatua sanguinea | C. pastinator | C. tenuirostris Cacatua leadbeateri | C. galerita Glossopsitta porphyrocephala | G. pusilla Polytelis swainsonii | P. anthopeplus Barnardius zonarius | B. barnardi Menura alberti | M. novaehollandiae Psophodes cristatus | P. occidentalis Cinclosoma punctatum | C. castanotum | C. alisteri | C. cinnamomeum

Display of the Golden-winged Manakin Masius chrysopterus

by D. W. Snow & B. K. Snow

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In July 1988, during a 6-week visit to La Planada, a forest reserve and biological research station in southwestern Colombia near the border with Ecuador, we spent 22 hours studying the courtship display and associated behaviour of the Golden-winged Manakin *Masius chrysopterus*, a species confined to humid subtropical forest of the Andes from western Venezuela to Peru. At the time we thought that nothing was known of its courtship; but on our return we found in our mail a recently published paper by Prum & Johnson (1987) on the Golden-winged Manakin in Ecuador, in which most aspects of the display were described in considerable detail. However, in their 164 hours of observation of territorial males Prum &

Johnson did not record copulation, and without this any account of the elaborate display behaviour of manakins is seriously incomplete. We were fortunate in seeing copulation three times, and in some particulars our observations differ from those recorded by Prum & Johnson. Hence it seems worthwhile to give a brief account of these observations, referring to Prum & Johnson for further details of those aspects where our

observations agree substantially or completely with theirs.

The adult male Golden-winged Manakin is strikingly different from any other member of the family. It is mainly black, except for a golden-yellow forehead and crown (the feathers of the forecrown projecting forwards, and those of the hindcrown and nape scale-like, becoming brownish or reddish posteriorly), a concealed pale yellow patch on throat and chest, and bright yellow under-wing coverts and inner webs of the middle flight-feathers, which show conspicuously in flight. Elongated feathers on either side of the crown project backwards to form two small lateral 'horns'. Like other manakins, the female is olive-coloured, paler below.

Prum & Johnson (1987) discuss the phylogeny and relationships of the monotypic genus *Masius* within the Pipridae. They show that it is almost certainly most closely related to *Corapipo*, and one of the most striking points of agreement between these two genera is that the males display on fallen logs on the forest floor, in contrast to all other manakins, which display on perches above the ground.

Spatial distribution of male territories

In the montane forest around La Planada, which is moderately or steeply sloping, we found Golden-winged Manakin males displaying in two areas. In the first area, at c. 1900 m, a single male displayed out of earshot of any other. In the other area, at c. 1800 m, three males displayed within earshot but not within sight of each other, roughly 100 m apart. The territories (areas within which all observed display took place, and where the birds spent the greater part of their time) measured, in two cases, about 25×18 and 25×15 m, with the long axis up and down gullies in the mountain side. Another was in a similar situation but was not measured; the fourth one was not studied. Censuses of forest birds at La Planada (C. Samper, pers. comm.) show that Golden-winged Manakins are more or less confined to forest on moderate slopes of $10-30^{\circ}$.

All our observations suggested that each display territory was in the undisputed possession of a single adult male. We never saw pairs of males displaying together, or visits by known males to display areas owned by

other males, as Prum & Johnson (1987) did on many occasions.

Display-logs

In each of the three territories at which we made observations, display was centred on a fallen log which was aligned up the slope of the gully or hill side. One was c. 85 mm in diameter and on a slope of c. 20°, another c. 200 mm in diameter and on a slope of c. 25°; the third was 93 mm in diameter, its slope was not measured. Each log was well covered with moss, but had on its upper surface a small patch that was smooth and free from moss, this cleared area being in one case 150 mm and in another 45 mm long. Males pick moss from their display-logs between bouts of

display, and also pick leaves and pieces of fern fronds growing adjacent to the part of the log where their display takes place. Our observations of this

behaviour agree with those of Prum & Johnson.

Prum & Johnson found that each male territory included 2–4 logs, the distance apart of which ranged from 5 to 40 m. We saw each male display at only one log; but, as indicated by his calls, the male which was watched for longest also displayed at two other places (presumably logs) that were out of sight. We have no reason to think that there was any difference in their use of display-logs between our birds and those studied by Prum & Johnson. What seemed significant, from our observations, was the downhill orientation of the logs, on slopes of 20–25°, and that this fits the habitat preference indicated by Cristián Samper's census data. As mentioned in a later section, the orientation of the log-approach display also depended on the slope of the log.

Elements of the courtship display

Prum & Johnson group these into (a) advertisement calling, (b) the logapproach display and display call, and (c) displays on the log. As our observations agree closely in most respects with theirs, in the following sections we avoid as far as possible going over all the same ground in detail, and concentrate on aspects of our observations that either amplify or in some way do not tally with theirs.

Advertisement calling. Males spent much the of the day calling from perches within their territory, often moving round the territory and calling from a variety of perches. The male that was watched for longest was present and calling in his territory for 91, 87 and 84% of the time during 3 one-hour observation periods between 11.30 and 15.30 on 20 July. During a continuous 3-hour observation period (11.00–14.00) on 22 July, he was present and calling for 79% of the time. Silent periods, when he

was probably foraging, were nearly all 1–3 minutes in length.

The call is a curious low-pitched, frog-like *nurrt* (sonagram in Prum & Johnson 1987), given singly. Intervals between calls are variable, sometimes (when the calling rate is high) only a few seconds, often much longer. We recorded a maximum calling rate of 8 calls per minute; 4–6 per minute was commoner. This is in good agreement with Prum & Johnson, who recorded a maximum rate of 9.6 per minute. A real difference between their data and ours is that their birds called from perches 2–4 m high, whereas ours regularly called from heights up to 11 m. Possibly this was in some way related to differences in the terrain and vegetation in the two study areas.

The *nurrt* is not loud, and so presumably serves to advertise the male's presence to conspecifics who are in the immediate vicinity rather than as a signal to attract distant birds. The calling bird is not visually conspicuous either, as it has its plumage ruffled, appearing almost wholly black, and does not make any striking movement. We noted that males often turn on their perch between calls. Prum & Johnson described the bird as popping its head up briefly exposing the yellow throat patch at the moment of calling. We described it as stretching slightly forward at the moment of calling, so that the yellow of the throat and upper breast was momentarily visible. Probably the slight head movement is both upward and forward.

Log-approach and display call. From a perch some distance away (10–15 m in most of the cases that we observed, but shorter distances recorded by Prum & Johnson), the male flies obliquely down to the display-log uttering a high-pitched whistle, lands on the log with a short two-note call, and immediately jumps back along the log in the direction from which he approached (for a distance of 30–40 cm according to Prum & Johnson, but see below; not measured by us), at the same time giving a third note which we transcribed as ker but which Prum & Johnson show is similar in structure to, but shorter than, the advertising nurrt. As it jumps, the bird turns in the air, to land facing its original landing place. The landing-and-jump is so rapid that the effect is of a 3-note call pk-k-ker, which in the tangled forested slopes where we watched served as a useful clue to the location of a display log.

Our observations agree in the main with Prum & Johnson's, but they do not mention a feature of this display which was very noticeable at the three logs where we saw it. The flight approach to the log was invariably from down hill, and it seemed a prerequisite of a suitable log that there should be a clear approach through the undergrowth from this direction. As already mentioned, the logs were aligned down the slope. Also Prum & Johnson do not mention that the jump on landing is a jump back in the direction of the approach flight, that is, a jump down the slope of the log. Their drawing (Fig. 2a) shows the bird jumping along the log in the same

direction as the approach flight.

Often, a male performed a succession of log-approaches one after the other, usually flying from the log out to the side, then moving round to a perch on the down-hill side from which to make the next approach-flight. Though on the down-hill side, these perches were well above the level of

the log, once an estimated 19 m above the log.

Log-displays. The displays which we saw performed on the log were what Prum & Johnson called the 'chin-down display' and 'side-to-side bowing'. Both are silent. The chin-down display is a motionless posture—the head lowered, with chin almost touching the log, tail up at an angle near the vertical, and plumage sleeked—held by the male immediately after the landing and jump-back in which the log-approach display culminates; it could perhaps be regarded as the final phase of that display. We saw it only at this point in the display sequence; it was regularly but not always performed, and lasted for only up to 2 seconds. It was evidently a more conspicuous feature of the displays seen by Prum & Johnson, as they saw it maintained for up to 20 seconds and say that it was "most often performed immediately following log approaches", so presumably also at other times.

Side-to-side bowing was the main display that we saw performed on the log. It was performed both in the presence of a female and when the male was alone on the log. Facing down hill, the male bows first to one side, over the edge of the log, then to the other side. On a narrow log he may simply swivel round between bows to alternate sides; on a wide log he takes small steps across the log to get in position for the bow to the other side. The body plumage is fluffed out and the back appears humped; the black 'horns' are erected; the orange hind-crest may stick up clear of the

nape but is not very conspicuous; the yellow on the wings is not visible. Thus the main impression, seen from the side, is an emphasis of the black plumage. From the front, the yellow fore-crest must be conspicuous. If a female is present she perches on the down-hill side of the male, close to him (c. 7–15 cm) and facing him. In one long sequence of side-to-side bowing, in the presence of a female and preceding mating, a total of 34 bows were made alternately from side to side. In another long sequence by a different male, which also preceded mating, the male began by making 3–4 bows to each side of the log, before going to the other side (taking a few steps across, the log being wide); then the bowing became more rapid and switched to single bows to each side. About 40 rapid alternating bows (c. 20 to each side) were performed before the sequence of actions leading to mating, described below.

Prum & Johnson's account of side-to-side bowing differs in some details. In particular, they describe the male as sometimes facing one side of the log and bowing alternately towards either end. We never saw this.

Mating. We saw mating on two occasions. At 13.05 hours on 30 July, a female came to a log on which a male had been actively displaying. She turned around several times, flew to a perch near by, then returned to the log, landing on the small area cleared of moss. The male arrived soon after, silently. He then performed a long bout of side-to-side bowing (described above) very close to the female, who was on his down-hill side facing him. He then flew off, and after c. 5 seconds returned from the usual down-hill direction, flew over the female and landed with a pk-k on her up-hill side, jumped back over her head to land on her down-hill side with a ker (the usual log-approach display), then mounted. After mating, the female remained where she was; the male, having dismounted on the up-hill side, again began side-to-side bowing, with single bows to each side; then flew off and returned in identical fashion and mounted again. After mating, which lasted 2–3 seconds, the female remained for about 10 seconds, then flew off. The male stayed a bit longer, slightly humpbacked (side-to-side bowing posture), then flew off and began calling.

On the other occasion, on 26 July, the sequence was essentially the same, except that in the course of the male's side-to-side bowing, which lasted about 2 minutes, the female made 10 flutters over the male and immediately back again. When on the down-hill side of the male, she crouched low and sometimes moved her head slightly from side to side. After the 10th flutter over the male and back, he flew off, out to the side, and then flew in from the down-hill end in the log-approach display and mated on landing. The female was crouching across the log at the place where it was barest of moss. After mating, the male did more side-to-side bowing, then again flew off and round and back again, but when he landed with the pk-k-ker the female had left.

A third sequence, seen on 29 July, involved the adult male who had mated on the 26th and a female-plumaged bird who was probably an immature male. After a long bout of side-to-side bowing (34 bows), during which the female-plumaged bird twice fluttered over the male and back, the male flew off; but when he returned and landed with the pk-k-ker the female-plumaged bird had moved slightly up the log. While

the male was in the chin-down posture, on the down-hill side, the female-plumaged bird briefly mounted him. Both birds then left. With no knowledge of the sex and status of the female-plumaged bird, this incident cannot be interpreted.

Other displays. Allowing for the fact that rapidly executed movements seen under difficult conditions and sometimes partially hidden by screening vegetation are often not clearly seen and, especially when first seen, are easily misinterpreted, we saw no displays that were definitely different from those described above. We did not see the display which Prum & Johnson call 'stamping'. For completeness we quote their description: "On several occasions males that were perched on display logs stamped their feet very rapidly for <1 sec, moving 2 or 3 cm ahead along the log. Although this display was infrequent and extremely short in duration, it appeared to have the stylized and nonfunctional qualities of a ritualized display behavior and was always performed while perched on the log in between bouts of side-to-side bowing."

Discussion

In the preceding sections we have mentioned a number of mainly minor discrepancies between our two accounts, involving details of display behaviour. At this stage in the study of a little known manakin it seems worthwhile highlighting such discrepancies, as experience shows that although manakin display repertoires are highly stereotyped, a long period of field study is needed before a full and accurate account can be given of the displays of any species. Difficult conditions of observation, and confusion in interpreting incompletely developed displays given in different contexts, combined with the rapidity of many of the movements,

are the chief problems encountered.

In addition to these minor discrepancies, a major difference between what we saw and what Prum & Johnson recorded concerns the social organization of the males. As already mentioned, all our males seemed to be in undisputed possession of a territory; we saw no interactions between them. Visitors to the display logs were all in female plumage and, from the evidence of their behaviour, were females (or, in one case, probably an immature male). Prum & Johnson, however, frequently saw pairs of males displaying simultaneously on a log, either two visiting males while the owner was absent or, more often, the resident male and a visiting immature male. On a number of occasions the two males performed perfectly coordinated alternating log-approach displays, and synchronized or coordinated side-to-side bowing displays.

Without further study it is impossible to explain this undoubted and striking difference in the behaviour of males at the two study sites, only about 80 km apart and linked by suitable forest habitat and so unlikely to have populations that are genetically very different. It seems most likely that, since Prum & Johnson did not see mating in spite of watching for much longer than we did, their observations (from 27 June to 28 July) may have been made a little before the main breeding season began (although a female mist-netted on 28 July had a well developed brood

patch), while ours were apparently made at the height of breeding. Very likely seasons vary somewhat not only from place to place but from year to year. Hence the frequent interactions between males at the display-logs at Prum & Johnson's study site may have been related to the establishment of dominance at what are probably traditional display-logs. If this was the case, it is of interest that the coordinated displays which develop between males in the pre-breeding period seem to parallel closely the coordinated displays between males in species of manakins in which such displays are a regular feature throughout the breeding season, e.g. members of the *Pipra aureola* species-group (Schwartz & Snow 1978, Robbins 1986).

Based on our observations alone, we would have had no hesitation in including *Masius* among the manakins in which males maintain individual spatially separated display territories in dispersed leks, such as the *Pipra serena* species-group, *Pipra pipra* and *Ilicura militaris*. Prum & Johnson, from their experience, conclude that the mating system of *Masius* is most like that of the *Pipra aureola* species-group. Clearly, further observations are needed.

Acknowledgements

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The Tree Sparrow Passer montanus in Sardinia

by J. D. Summers-Smith

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The first breeding record for the Tree Sparrow in Sardinia was of two pairs nesting in the tower of the fortress of Cagliari in 1898 (Bonomi 1899). Before that it had been known only as a winter visitor, for example an adult male at Decimomannu (17 km north-west of Cagliari) on 20.10.1896 (Giglioli 1907). There have been regular reports of breeding in Cagliari since the first record: breeding 1905 (Giglioli 1907), 1906 (Martorelli 1906), 1921–22 numerous breeder in Cagliari and its